Nicholls, Ed. (Springer-Verlag, Berlin, 1982), p. 71.
5. L. I. Benowitz et al., J. Neurosci. 1, 300 (1981).
6. D. Giulian, H. Des Ruisseaux, D. Cowburn, J. Biol. Chem. 255, 6494 (1980).
7. A. M. Heacock and B. W. Agranoff, Proc. Natl. Acad. Sci. U.S.A. 73, 828 (1976).
8. _____, Neurochem. Res. 7, 771 (1982).
9. W. Quitschke and N. Schechter, Brain Res. 258, 69 (1983).
10. J. H. P. Skene and M. Willard, Cell Biol. 89, 86 (1981).
11. G. E. Landreth and B. W. Agranoff, Brain Res. 118, 299 (1976).
12. _____, ibid. 161, 39 (1979).
13. P. M. Richardson, U. M. McGuiness, A. J. Aguayo, Nature (London) 284, 264 (1980).
14. C. C. Kao, L. W. Chang, J. M. B. Bloodworth, Exp. Neurol. 54, 591 (1977).
15. D. Neumann, A. Yerushalmi, M. Schwartz, Brain Res. 272, 237 (1983).
16. I. Rachailovich and M. Schwartz, ibid. 306, 149 (1984).
17. J. H. P. Skene and E. M. Shooter, Proc. Natl. Acad. Sci. U.S.A. 80, 4169 (1983); M. A. Deaton and J. A. Freeman, Soc. Neurosci. Abstr. 9, 693 (1983).
18. M. Nieto-Sampedro et al., Science 217, 860 (1982).
19. M. Belkin et al., Invest. Opt. Vis. Sci. 25 (Suppl.), 249 (1984).
20. M. Schwartz and B. W. Agranoff, Brain Res. 3, 29 (1981).
21. Supported by grants to M.S. from the Israel Ministry of Health and by the trustees of the Pearl M. Levine estate, S. Kaplan and J. Kaplan, in association with the California Chapter of the National Spinal Cord Injury Association. M.S. is an incumbent of Helena Rubinstein Career Development Chair.

16 August 1984; accepted 3 December 1984

Habitat Selection in a Clonal Plant

Abstract. Rhizomatous growth may permit the nonrandom placement of ramets into different environments, but whether clonal plants are able to use this means to exercise adaptive habitat choice is not known. Western ragweed (Ambrosia psilostachya) plants are shown to preferentially colonize nonsaline soil over saline soil patches, and clones with the strongest preference for nonsaline soil are those least able to grow when restricted to saline conditions. In clonal plant species, nonrandom associations of genotypes with specific environments may thus reflect habitat selection by plants as well as selective mortality imposed by different habitat patches.

Active habitat selection is vital to the behavioral ecology of many animals. Although immobility precludes habitat selection by individual growing plants, it has been suggested that phenomena analogous to habitat selection could occur in clonal plant species with rhizomatous growth (1). The selective placement of vegetative units into nutrient-rich or otherwise optimal microsites may enable clonal plants actively to choose habitats for future growth and reproduction. However, there is little experimental evidence that adaptive habitat choice indeed occurs in rhizomatous plants (2). I report that plants of the perennial herb western ragweed (Ambrosia psilostachya: Compositae) (3) selectively colonize contrasting habitat patches in a complex environment. Furthermore, genotypes of this species differ in their degree of discrimination between optimal and suboptimal patches, indicating the potential for habitat preference to evolve in response to natural selection.

On natural saline flats in the Great Plains, clones of western ragweed occupy a wide range of soil salinities (4). Salt depresses plant growth (4), but there is extensive genetic variation in salt tolerance in this species (5). Field transplants of clones spanning a range of tolerance levels indicate that ramet survivorship in saline habitats is greater among more salt-tolerant genotypes (6). Soil salinities may be sharply heterogeneous on a local scale (<0.5 m) (4); thus, a capacity for

nonrandom colonization of different soil types would have important consequences for the process of natural selection in ragweed populations.

The following experiment was conducted to evaluate (i) whether western ragweed was able to select between saline and nonsaline microhabitats and (ii) the magnitude of genetic (clonal) variation for habitat preference in this species. Six replicate ramets (stems) of nine distinct clones (7) were individually rooted in low-salinity soil in the center of

Table 1. Habitat preferences of nine western ragweed clones in the greenhouse experiment. Preference was calculated as the proportion of total shoots emerging in nonsaline soil.

Clone	Rank of salt tolerance*	Proportion of emerged shoots in nonsaline end†
A	1	0.60 (216)‡
B	4.5	0.64 (210)
C	2	0.71 (55)
D	4.5	0.73 (200)
E	6	0.73 (177)
F	3	0.89 (53)
G	8	0.89 (95)
H	9	0.92 (80)
I	7	0.96 (74)
Total		0.74 (1160)

*High tolerance = 1. †χ^2 texts indicate that every clone deviates significantly from equal shoot placement in the two habitats ($P < 0.005$). ‡Numbers in parentheses are total emerged shoots for each clone in saline and nonsaline ends, summed over six pots (five for B).

long narrow pots (18 by 46 by 13 cm) in a greenhouse. A gradient in soil salinity was maintained by repeatedly watering one end of the pot (15 cm) with 1 percent NaCl (8) and flushing the rest of the pot with tap water to prevent salt accumulation (4). Each plant thus had equal opportunity to invade saline and nonsaline patches at the opposite ends of its pot. After 3 months, the plants had produced underground rhizomes in the saline and nonsaline sections of every pot, and numerous shoots began to emerge from the soil surface. Emergence of shoots declined after 4 months; each plant's habitat preference was then calculated as the proportion of all shoots that emerged in nonsaline soil. A value of 0.5 signified equal placement of shoots in both habitats (no preference); values less or greater than 0.5 indicated respective preference for saline or nonsaline soil. Finally, the distribution of shoots that failed to emerge was quantified.

The initiation and development of new vegetative shoots was strongly biased towards nonsaline soil. Of 2730 total shoots initiated in all 53 pots (average 51.5 shoots per pot), 67 percent occurred in nonsaline soil ($\chi^2 = 319$, $P < 0.0001$). Furthermore, the proportion of shoots that emerged from the soil surface was significantly greater in nonsaline (47 percent) than in saline soil (34 percent) ($\chi^2 = 18.06$, $P < 0.001$). The population of emerging shoots was thus strongly concentrated in nonsaline soil ($\chi^2 = 266$, $P < 0.0001$) (Table 1). Mortality of shoots before emergence from the soil was negligible (<10 percent for all clones in both habitats) and did not account for this bias.

All nine genotypes showed a significant preference for nonsaline habitat, yet the intensity of discrimination varied widely among clones (Table 1), ranging from moderate (60 percent of shoots in nonsaline soil: clone A) to very strict (>90 percent in nonsaline soil: clones H and I). The heritability (broad sense) of habitat preference was 0.39 (95 percent confidence interval: 0.16, 0.73) (9), indicating substantial genetic control over variation in this trait. In addition, the nine clones in this experiment had previously been evaluated for salt tolerance (that is, growth rate when confined to saline soil) (5). Less salt-tolerant genotypes showed a significantly higher concentration on nonsaline soil (Spearman's $r_s = -0.75$; $n = 9$; $P < 0.05$) (Table 1).

These patterns of differential shoot placement may reflect (i) the direct suppression of plant growth by saline soil conditions or (ii) the facultative reduction by plants of resource allocation for

growth in saline soil patches, or both. There is independent evidence for the involvement of mechanism (ii) in the preferential colonization of nonsaline soil observed in this experiment. In a field transplant experiment where ramets of these clones were confined to uniform conditions of high (0.8 to 1.4 percent) or low (<0.2 percent) salinity (6), all nine genotypes proved capable of vegetative proliferation in both soil types. For every clone the difference in shoot production per surviving ramet in saline compared to nonsaline soil was smaller than the difference between the two ends of each pot in the greenhouse "choice" experiment (sign test, $n = 9$, $P < 0.002$). Thus, the colonization rate of two contrasting habitats differed more strongly when individual plants were offered a "choice" (Table 1) than when they were not.

Opportunities for habitat selection in natural populations depend on the rate of rhizome growth into new territory. In the field transplant experiment, rhizome growth in nonsaline soil was extremely limited; only 3 percent of daughter ramets occurred at 20 cm or farther from their parent plants; (range, 0 to 60 cm; $n = 1130$). Dispersal in saline soil was dramatically higher, with 28 percent of all ramets appearing at 20 cm or farther from their parents (range, 0 to 80 cm; $n = 982$). There was striking genotypic variation in shoot dispersal in saline soil: clonal mean dispersal distances ranged from 5.0 to 31.6 cm, and clonal differences accounted for 30 percent of the total variance in shoot dispersal distance (10). The greater dispersal achieved by plants in saline soil was unexpected, since salt severely depresses plant biomass accumulation. However, this commitment to extensive rhizomatous spread increases the rate at which plants in saline soil encounter new territory, thereby increasing the probability of locating favorable microsites. Clonal differences in dispersal result in large differences in the rate of sampling new habitats and ultimately determine each genotype's opportunity to exercise adaptive habitat choice.

The often striking associations between plant genotypes and local environments are usually thought to depend for their maintenance on high mortality rates among nonadapted immigrant genotypes (11). Habitat selection may permit clonal plants to become genetically segregated among habitats without the severe energetic and demographic costs of selective mortality. The capacity of western ragweed (4) and many other clonal species

(12) to share resources among ramets through rhizome connections further increases the efficiency of colonization and habitat exploration in these species. The results show that active habitat choice could be a significant mechanism producing genotype-microenvironment correlations in natural populations of clonal plants. It is not yet possible to distinguish between this process and selective mortality.

AMY G. SALZMAN
Department of Biology, University of Chicago, 915 East 57 Street, Chicago, Illinois 60637

References and Notes

1. R. Turkington and J. L. Harper, *J. Ecol.* **67**, 245 (1979); A. D. Bell and P. B. Tomlinson, *Bot. J. Linn. Soc.* **80**, 125 (1980); R. E. Cook, *Am. Sci.* **71**, 244 (1983); A. D. Bell, in *Perspectives on Plant Population Ecology*, R. Dirzo and J. Sarukhan, Eds. (Sinauer, Sunderland, Mass., 1984).
2. R. A. Schellner, S. J. Newell, O. T. Solbrig, *J. Ecol.* **70**, 273 (1982).
3. Vegetative proliferation in *A. psilostachya* occurs by production of root buds on thickened roots [R. L. Peterson, in *The Development and Function of Roots*, J. G. Torrey and D. T. Clarkson, Eds. (Academic Press, New York, 1975)]. These are functionally equivalent to other dispersive vegetative structures such as rhizomes, a term that I use here in its broad sense [see A. D. Bell and P. B. Tomlinson in (*1*)].
4. A. G. Salzman and M. A. Parker, *Oecologia* **65**, 273 (1985). *Ambrosia psilostachya* occurs in soil salinities up to 1.5 percent in natural populations.
5. Salt tolerance index was calculated as the mean biomass accumulation after 6 weeks' growth in 1 percent NaCl saline soil of four cloned replicates per genotype in a common greenhouse environment. Assays of over 100 *A. psilostachya* genotypes indicate a fourfold range in salt tolerance index.
6. There were 13 to 16 replicates of 13 genotypes transplanted into saline (0.8 to 1.4 percent salinity) and nonsaline soil (<0.2 percent salinity) in Lancaster County, Nebraska. Overall survivorship through two growing seasons in saline soil was 0.42 ($n = 205$), significantly lower than 0.83 in nonsaline soil ($n = 162$; $\chi^2 = 62.63$; $P < 0.0001$). Clonal mean survivorship showed a significant positive regression on salt tolerance in saline soil (range 0.25 to 0.60; analysis of variance on arcsin square-root transformed data: $F = 14.95$; d.f. $= 1,11$; $P < 0.003$; $r^2 = 0.58$) but not in nonsaline soil (range 0.54 to 1.00; $F = 0.87$; d.f. $= 1,11$; $P > 0.35$; $r^2 = 0.07$). Soil salinities were determined as described by L. A. Richards [*Diagnosis and Improvement of Saline and Alkaline Soils: Agricultural Handbook 60* (Government Printing Office, Washington, D.C., 1954)].
7. Genotypes were distinguished by numerous markers including leaf shape, pubescence, growth form, and phenology when grown in a common environment.
8. Sodium chloride constitutes more than 90 percent of dissolved solids at these field sites [L. R. Kister and J. C. Mundorff, *Geol. Surv. Water-Supply Pap. 1669-H* (1954); I. A. Ungar *et al.*, *Am. Midl. Nat.* **8**, 564 (1969)].
9. D. S. Falconer, *Introduction to Quantitative Genetics* (Longman, New York, 1981); R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, 1969), pp. 204–213. Analysis of variance (ANOVA) indicates highly significant variation among clones in the proportion of shoots in nonsaline soil (range among pots, 0.41 to 1.00; ANOVA on arcsin square-root transformed data: $F = 4.76$; d.f. $= 8,44$; $P < 0.0003$).
10. Analysis of variance on clonal differences in shoot dispersal distance in saline soil: range 0 to 80 cm; $F = 35.81$; d.f. $= 11$, 970; $P < 0.0001$.
11. S. K. Jain, A. D. Bradshaw, *Heredity* **21**, 407 (1966); J. L. Hamrick and R. W. Allard, *Proc. Natl. Acad. Sci. U.S.A.* **69**, 2100 (1972); R. W. Snaydon and M. S. Davies, *Heredity* **37**, 9 (1976); J. A. Silander, *Science* **203**, 658 (1979); see R. Turkington and J. L. Harper in (*1*) and A. D. Bradshaw, in *Perspectives on Plant Population Ecology* in (*1*).
12. J. W. Ashmun, R. J. Thomas, L. F. Pitelka, *Ann. Bot.* **49**, 403 (1982); S. J. Newell, *Bull. Torrey Bot. Club* **109**, 306 (1982); D. C. Hartnett and F. A. Bazzaz, *Ecology* **64**, 779 (1983); J. C. Noble and C. Marshall, *J. Ecol.* **71**, 865 (1983).
13. I thank D. Schemske and M. Parker for extensive help and C. Boake, S. Via, M. Wade, and two anonymous reviewers for helpful comments. S. Yamins, W. Schroeder and B. McCarthy assisted in the greenhouse. A. Joern and L. Vescio provided frequent hospitality in Nebraska. Research supported by Sigma Xi, the Eli A. Nierman Foundation, and PHS grant GN 07197, Training Program in Genetics and Regulation.

10 September 1984; accepted 14 February 1985

Amygdalectomy Impairs Crossmodal Association in Monkeys

Abstract. Monkeys trained on both visual and tactual versions of an object memory task (delayed nonmatching-to-sample) received bilateral ablations of either the amygdaloid complex or the hippocampal formation of the brain. Although both groups performed well on the two intramodal versions (visual-to-visual and tactual-to-tactual), the amygdalectomized monkeys were severely impaired relative to the hippocampectomized monkeys on a crossmodal version (tactual-to-visual). The findings suggest that the amygdala is critical for certain forms of crossmodal association and that the loss of such associations underlies many of the bizarre behaviors that make up the Klüver-Bucy syndrome.

The amygdaloid complex has long been considered essential for the sensory arousal of affective responses, that is, for the association of sensory stimuli with emotions (1, 2). We now report that the amygdala is also essential for associations that have no obvious emotional content. Amygdalectomized monkeys, like their controls, accurately recognized objects both visually and tactually; yet, unlike their controls, they failed to recognize by vision an object they had just examined by touch. This crossmodal impairment may help explain some of the dramatic and puzzling effects of amygdalectomy on naturally occurring behavior (1).

Six cynomolgus monkeys (*Macaca fascicularis*) were first trained on a one-trial visual memory task—delayed nonmatching-to-sample—with a set of 40 visually and tactually distinctive objects that differed in color, size, shape, texture, and compressibility (3). The objects